

Phosphorus Bioavailability following Incorporation of Green Manure Crops

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ABSTRACT

Incorporating green manure crops into soil may increase P bioavailability for succeeding crops. We conducted a greenhouse study to evaluate the effects of green manures on biomass and P utilization of a succeeding grain sorghum [*Sorghum bicolor* (L.) Moench] crop. Four perennial forages and four winter annual cover crops were grown in pots, killed, and incorporated into the soil before planting sorghum in the same pots. Sorghum P uptake was positively correlated with perennial forage P uptake. Among winter cover crops, sorghum P uptake following white lupine (*Lupinus albus* L.) was lower than in all other treatments, including the control (no previous cover crop), even though lupine biomass, N content, and P uptake were two to three times greater than those of the other winter cover crops. Phosphorus uptake differed slightly among the other three winter cover crops but sorghum P uptake was not correlated to winter cover crop P uptake. Thus, among winter cover crops, plant type rather than P uptake seemed to influence the subsequent sorghum crop's P uptake. However, sorghum biomass following the three winter cover crops other than lupine was greater than sorghum biomass in the control treatment, indicating that there was a beneficial cover crop rotation effect among these three winter cover crops. Soil samples were collected and analyzed for Bray-1 P when green manure crops were planted, when they were incorporated into the soil, when sorghum was planted and when sorghum was harvested. These data showed that the Bray-1 soil P test has little potential to predict differences in P uptake and release among different types of green manures and it has limited potential to predict P uptake by sorghum following incorporation of green manures.

GREEN MANURE CROPS can increase cropping system sustainability by reducing soil erosion and ameliorating soil physical properties (MacRae and Mehuys, 1985; Smith et al., 1987), by increasing soil organic matter and fertility levels (Doran and Smith, 1987; Power, 1990), by increasing nutrient retention (Staver and Brinsfield, 1998; Drinkwater et al., 1998; Dinnes et al., 2002), by helping control weeds (Teasdale, 1998), and by reducing global warming potential (Robertson et al., 2000). Research on the effects of cover cropping on soil fertility in temperate regions has focused largely on the ability of cover crops to supply N to succeeding crops (e.g., Smith et al., 1987; Sustainable Agriculture Network, 1998), while the potential of green manures to affect P fertility of succeeding crops in temperate regions has remained largely uninvestigated (Doran and Smith, 1987; Power, 1990; Sustainable Agriculture Network, 1998).

Green manures may enhance P nutrition of succeeding crops via a number of mechanisms. Green manure

crops may convert relatively unavailable native and residual fertilizer P to chemical forms more available to succeeding crops. Alfalfa (*Medicago sativa* L.), red clover (*Trifolium pratense* L.), sweet clover [*Melilotus officinalis* (L.) Lam.], and lupine can absorb more P than most other crops from soils testing low in P (DeTurk, 1942; Russell, 1973; Gardner et al., 1982; Braum and Helmke, 1995). On decomposition, organic P in green manure tissues could provide a relatively labile form of P to succeeding crops, thus providing a larger pool of mineralizable soil organic P to supplement soluble inorganic P pools (e.g., Tiessen et al., 1994). Organic P (P_o) mineralization supplies significant amounts of plant P in grasslands (Cole et al., 1977), and perhaps in some perennial (Havlin et al., 1984) and organic (Oehl et al., 2001) agricultural systems.

Decomposition processes, which are stimulated when green manure residues are incorporated into the soil, can further increase P availability by releasing CO_2 , which forms H_2CO_3 in the soil solution, resulting in the dissolution of primary P-containing minerals (Tisdale et al., 1985). Also, organic acids released during decomposition may help dissolve soil mineral P (Sharpley and Smith, 1989). In soils with high P-fixing capacities, organic compounds released during decomposition processes may increase P availability by blocking P-adsorption sites (Easterwood and Sartain, 1990) or via anion exchange (Kafkafi et al., 1988). Some amino acids, however, can increase P adsorption by soil (Kafkafi et al., 1988). Repeated incorporation of green manures can also result in decreased soil bulk density and increased soil aggregation and moisture retention, all factors that may help increase P uptake by succeeding crops via their effects on increased root and mycorrhizal growth (MacRae and Mehuys, 1985).

Adding plant residues to soil can increase soil test P (Black, 1973; Bumaya and Naylor, 1988; McLaughlin et al., 1988a; Li et al., 1990; Vanlauwe et al., 2000), increase P_o (Dalal, 1979), increase P uptake by succeeding plants (Blair and Boland, 1978; Till and Blair, 1978; Dalal, 1979; Thibaud et al., 1988; Vanlauwe et al., 2000), and decrease soil P sorption (Singh and Jones, 1976; Bumaya and Naylor, 1988). However, plant P availability does not always increase following green manure incorporation (McLaughlin and Alston, 1986; Groffman et al., 1987; Bumaya and Naylor, 1988; McLaughlin et al., 1988b) since the soil microbial biomass and soil sorption processes compete for available P (e.g., Cole et al., 1977; White and Ayoub, 1983). Most studies report that net P immobilization occurs when the total P concentration of plant tissues incorporated into soil is below 2 to 3 g kg^{-1} (Yadvinder-Singh et al., 1992), although Bumaya and Naylor (1988) report that net P mineralization oc-

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curred when plant tissue P concentrations were as low as 1 g kg^{-1} . Increases in soil P fertility following green manures may be difficult to detect since conventional soil P tests do not assess readily mineralizable P_o (e.g., Campbell et al., 1984; Tiessen et al., 1994).

The objectives of this greenhouse study were (i) to evaluate the effects of green manure growth and subsequent soil incorporation on the P uptake of a succeeding sorghum crop, and (ii) to evaluate the ability of the Bray-1 soil P test to measure relative soil P bioavailability for green manure crops and for a subsequent sorghum crop. We hypothesized that sorghum biomass and P uptake would be highest following green manure crops with the highest P contents.

MATERIALS AND METHODS

We collected soil from the top 30 cm (full A1 and top 10 cm of the B1 horizons) of a Smolan silt loam (fine, smectitic, mesic Pachic Argiustolls) in Manhattan, KS. The site had been cropped to soybeans for the three previous years. The soil was stored at field moisture and room temperature for about 12 wk before we sieved (2 mm) and mixed it extensively with a shovel. We measured soil characteristics on soil samples taken immediately before the start of the experiment. Soil pH (1:1 w/v) (McLean, 1982) was 6.7 and Bray-1 extractable P (Olsen and Sommers, 1982) was 17 mg kg^{-1} . This P value is in the medium range for Kansas soils, indicating that most field crops will respond only slightly and not consistently to additional fertilizer P applications (Whitney, 1998).

To provide ample rooting volume to the plants, we designed and used pots made of 10-cm diam. PVC pipe, 60 cm tall. Drainage was provided by securing a cap with drainage holes on the bottom of each tube. Soil was packed into the pots to an average bulk density of 1.24 Mg m^{-3} by dropping a 2.5-kg weight from a height of 35 cm five times on successive equivolume (about 0.5 L) layers of soil. The surface of each layer was then scratched to minimize formation of a compacted zone between layers (Bohm, 1979). Pots were filled to within 1 cm of the top and soil moisture was maintained at approximately field capacity ($0.33 \text{ g water g soil}^{-1}$) by weighing individual pots and replacing lost water when necessary.

We took soil samples for Bray extracts at four times: when green manure crops were planted, when they were incorporated into the soil, when sorghum was planted, and when sorghum was harvested. The first sample was taken from the bulk soil during pot filling and the latter three samples were taken from holes that we had drilled through the PVC before filling the pots. Each pot had four equally spaced 2.5-cm diam. soil sampling ports 8.5 cm from the top of the tube. Sampling ports were covered with duct tape before filling the pots with soil and soil samples were taken by removing the tape and extracting a 2.5-cm diam. and 4 cm long soil core using a drill bit. We refilled the resulting hole with soil stored since the beginning of the experiment. Each pot also had two additional soil-sampling ports, one at 30 cm and one at 54 cm from the top of the pot. When sorghum was planted three soil samples, one taken from each depth, were composited to estimate soil N (2 M KCl-extractable $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$, determined by colorimetry [Keeney and Nelson, 1982]).

We conducted two crop rotation experiments, one using perennial forages as green manures and one using winter annual cover crops. In each experiment, green manure shoots and roots were incorporated into the same soil in which they were grown before planting grain sorghum (cultivar TX2752 \times TX430). Perennial forages were 'Riley' alfalfa, 'Nitro' alfalfa,

'Medium Red' red clover, and 'Yellow Blossom' yellow sweet clover. Winter cover crops were: 'Hope' white lupine, 'common' Austrian winter pea [*Pisum sativum* L. subsp. *sativum* var. *arvense* (L.) Poir], 'common' hairy vetch (*Vicia villosa* Roth.), and 'Arkan' winter wheat (*Triticum aestivum* L.). These perennial forages and winter cover crops represent species and varieties commonly used or that have shown some potential for use in Kansas. We selected Nitro alfalfa, a non-dormant perennial that winter kills, because it has a larger root (greater length and diameter) than more conventional varieties (Pfarr, 1988), a characteristic that can increase P uptake rates (Barber, 1984).

Because seed size affects root growth (Bohm, 1979) and, therefore, P uptake (Barber, 1984), we sieved seeds and planted only medium-sized seeds. Seeds were germinated in vermiculite and four plants of each cover crop were transplanted into each of eight replicate pots 6 to 12 d after germination. Four pots with no cover crops served as controls in each experiment. All legumes were inoculated with the appropriate *Rhizobium* species. Sodium vapor lights supplemented natural lighting for 12 h each day. Air temperature was set at 25°C . The pots were arranged in a randomized complete block design with four replicates.

Perennial forages were killed 59 d and winter cover crops were killed 34 to 37 d after transplanting by cutting shoots at the soil surface. Plants in four replicate pots of each treatment were sacrificed to measure root and shoot biomass and nutrient contents. Roots were harvested by splitting the pots lengthwise with a circular saw and washing the roots from the resulting soil cores using tap water under pressure. Shoots and roots were separated, dried at 65°C , digested in $\text{HNO}_3\text{-HClO}_4$, and analyzed for N and P concentration using a Technicon AutoAnalyzer (Technicon, Tarrytown, NY; Thomas et al., 1967; Technicon Industrial Systems, 1977). Phosphorus concentrations of the winter cover crop seeds were determined in a similar manner and we calculated seed P content (P concentration \times biomass). Since winter cover crop seeds of each species were a different size and were large, we report two different P contents for cover crops: P uptake and adjusted P uptake. P uptake is (root P concentration \times root biomass) + (shoot P concentration \times shoot biomass). Adjusted P uptake is P uptake – seed P content. Since the perennial forage seeds are very small we assumed that their P content is insignificant relative to plant P uptake and we report only P uptake for perennial forages. For sorghum, we report only P uptake since all sorghum seeds were similar in size.

Cover crop shoots in the remaining four pots were returned to the soil and allowed to begin decomposing before planting sorghum seeds. We first measured shoot wet weights, cut the shoots into 1-cm lengths, removed the top 10 cm of soil from each pot along with associated roots, mixed the cut shoots with the soil and roots, and returned the mixture to the pot. Soil moisture was maintained at about field capacity for 32 d for perennial forage residues and for 39 d for winter cover crop residues. Five sorghum seeds were then planted near the center of each pot. After 5 to 9 d we removed all but one of the sorghum plants. Soil N tests taken at sorghum planting were used to determine if N fertilizer needed to be applied to soils in which green manures had been incorporated (Whitney, 1998). We also planted sorghum in the green manure control pots but fertilized these pots with NH_4NO_3 at a rate equivalent to 90 kg N ha^{-1} (P. Bramel-Cox, ICRISAT, personal communication, 1989). We harvested sorghum roots and shoots after 38 d in the perennial forages experiment and after 40 d in the winter cover crops experiment.

We used the general linear models procedure to determine effects of cover crops on soil P and the subsequent sorghum

Table 1. Green manure crop nutrient concentrations, biomass, N content, and P uptake for plants (shoots + roots) grown in pots in a greenhouse.

Crop	Tissue concentration		Biomass	N content	P uptake	Adjusted P uptake†
	N	P				
	g kg ⁻¹					
			g pot ⁻¹	mg pot ⁻¹		
<u>Perennial forages</u>						
Riley alfalfa	24.1	1.82	5.89	147	10.7	ND‡
Nitro alfalfa	25.0	1.75	6.77	169	11.9	ND
Red clover	24.6	1.67	6.07	157	10.1	ND
Sweet clover	24.3	1.54	7.60	189	11.7	ND
LSD _{0.05}	NS§	NS	0.79	20	1.3	
<u>Winter cover crops</u>						
Lupine	40.2	2.26	6.35	255	14.3	10.9
Pea	40.5	2.38	2.57	104	6.1	4.3
Vetch	47.6	2.57	2.05	98	5.3	4.9
Wheat	31.3	2.35	2.68	84	6.3	6.0
LSD _{0.05}	2.5	0.18	0.37	15	0.9	0.9

† Adjusted P uptake = P uptake – P seed content.

‡ ND = not determined.

§ NS = not statistically significant.

crop and separated means using LSMEANS (SAS Institute, 2001). To analyze soil P data a mixed model, repeated measures analysis was used (SAS Institute, 1996).

RESULTS

Green Manures

Perennial Forages Experiment

There were no differences in tissue P and N concentrations among the four perennial forage crops (Table 1). There were, however, small differences in P uptake among perennial forages, with sweet clover and Nitro alfalfa having higher P uptake than red clover ($P < 0.05$). Sweet clover produced more biomass ($P < 0.005$) and had higher N content ($P < 0.005$) than did the other three cover crops. In contrast with longer-term field studies (Pfarr, 1988), Nitro alfalfa did not have significantly greater root biomass than Riley alfalfa (data not shown). However, Nitro alfalfa did produce more total (root + shoot) biomass and had higher N content than did Riley alfalfa.

Winter Cover Crops Experiment

All three winter cover crop legumes had higher tissue N concentrations than did wheat (Table 1). Cover crop P uptake and N content, however, varied with plant biomass. For example, although vetch had the highest tissue P and N concentrations, vetch had the lowest biomass ($P < 0.001$) and among the lowest N contents ($P < 0.001$), P uptake ($P < 0.001$), and adjusted P uptake ($P < 0.001$) (Table 1). On the other hand, lupine, which had lower tissue N and P concentrations than vetch, had biomass, N content, and P uptake about two to three times greater than those of pea, vetch, and wheat.

Sorghum Following Green Manures

Perennial Forages Experiment

Sorghum P uptake was greater following Nitro alfalfa than in all other treatments ($P = 0.003$) (Table 2). Sorghum P uptake following Riley alfalfa and red clover were greater than following no cover crop but sorghum P uptake following sweet clover was not different than

Table 2. Sorghum nutrient concentrations, biomass, N content, and P uptake when grown in pots in a greenhouse following green manure crops. All values are for shoots + roots.

Previous crop	Tissue concentration		Biomass	N content	P uptake
	N	P			
	g kg ⁻¹				
Perennial forages					
Riley alfalfa	8.8	0.98	15.6	137	15.2
Nitro alfalfa	8.7	1.08	16.1	140	17.4
Red clover	9.4	0.96	15.5	145	15.0
Sweet clover	9.9	0.98	14.8	147	14.5
Control (no cover crop)	18.6	1.22	10.5	192	12.6
LSD _{0.05}	2.1	0.14	1.6	15	2.0
Winter cover crops					
Lupine	23.2	1.59	7.45	173	11.9
Pea	19.1	1.56	10.1	191	15.7
Vetch	18.5	1.61	9.92	184	16.0
Wheat	16.7	1.39	10.7	179	14.8
Control (no cover crop)	21.2	1.99	8.32	172	16.3
LSD _{0.05}	4.1	0.21	1.5	NS†	2.3

† Not statistically significant.

Table 3. Correlation coefficients between biomass, N content, and P uptake of four perennial forage green manures and P uptake and biomass of a succeeding sorghum crop.

Perennial forage green manure characteristics	Sorghum characteristics	$P > F^\dagger$	r
P uptake	P uptake	0.07	0.47
N content	P uptake	0.57	0.15
Biomass	P uptake	0.54	0.16
P uptake	Biomass	0.18	0.35
N content	Biomass	0.84	0.05
Biomass	Biomass	0.86	0.05

† Probability of a greater F value.

sorghum P uptake following no cover crop. Perennial forage P uptake and sorghum P uptake were correlated at $P = 0.07$ (Table 3). Perennial forage N content and biomass were not correlated with sorghum P uptake; and perennial forage P uptake, N content, or biomass was not correlated with sorghum biomass.

Soil inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) levels when sorghum was planted were similar among all cropped pots (42–43 mg kg⁻¹), indicating that no additional fertilizer was needed to reach sorghum grain yields of 11 290 kg ha⁻¹ (Whitney, 1998). Sorghum in the control pots was fertilized with NH_4NO_3 25 d after planting (13 d before harvest), at which point the sorghum plants visually were smaller in the control pots than in the cropped pots. At harvest, sorghum biomass and P uptake were much lower and N content was much higher in control pots than in any other pots, probably because of the late fertilization date.

Winter Cover Crops Experiment

Sorghum P uptake and biomass following lupine were lower than sorghum P uptake and biomass following all other winter cover crops (Table 2; P uptake ANOVA $P < 0.05$; biomass ANOVA $P < 0.005$). Sorghum P uptake following lupine was even lower than sorghum P uptake following no cover crop. Among other cover crops, sorghum biomass was higher following wheat, pea, and vetch than following no cover, but there were no differences in sorghum P uptake among these four treatments. There were significant negative correlations between cover crop characteristics and sorghum P uptake and biomass (Table 4). These negative relationships were due to lupine's unique behavior (high lupine biomass, N content, and P uptake, and low succeeding sorghum biomass and P uptake): All correlation lines were essentially defined by two points, with the lupine values clustered at one end of the line and values for all other winter cover crops clustered at the other end of the line. Therefore, we ran all correlation analyses without the lupine data to determine if there were any relationships between characteristics of the other three cover crops and sorghum biomass and P uptake. These analyses show that cover crop characteristics and sorghum P uptake and biomass were not related (Table 4).

Soil inorganic N levels when sorghum was planted were affected by differences in cover crop N contents and were highest in soils containing lupine residues (57 mg kg⁻¹), intermediate in soils containing pea resi-

dues (39 mg kg⁻¹), and lowest in soils containing vetch (31 mg kg⁻¹), wheat (28 mg kg⁻¹), or no residues (24 mg kg⁻¹; $P < 0.005$; $\text{LSD}_{0.05} = 12$). The observed soil inorganic N levels indicate that legumes provided sufficient N to reach sorghum grain yields of at least 9410 kg ha⁻¹ (150 bu A⁻¹) (Whitney, 1998). There were no differences in sorghum N content among the five treatments ($P = 0.55$; Table 2).

Bray-1 Soil Phosphorus

Perennial Forages Experiment

Bray-1 soil P in control soils stayed relatively constant during perennial forage growth and decomposition (Fig. 1A). Bray-1 soil P in cropped soils; however, it decreased by about 4 mg kg⁻¹ in all soils during perennial forage growth ($P < 0.0001$) and increased by about 2 to 3 mg kg⁻¹ during perennial forage residue decomposition ($P < 0.005$). Bray-1 soil P values at the time of sorghum planting were lower in cropped soils than in the uncropped control soils ($P < 0.0001$). During sorghum growth, Bray-1 P decreased by 4 to 5.6 mg kg⁻¹ in all treatments, with only slight differences among treatments ($P = 0.08$).

To determine if changes in Bray-1 soil P reflected plant P uptake we ran three correlation analyses. There were no relationships between perennial forage P uptake and decrease in Bray-1 soil P during perennial forage growth ($P = 0.61$), between perennial forage P uptake and increase in Bray-1 soil P during perennial forage decomposition ($P = 0.76$), and between sorghum P uptake and decrease in Bray-1 soil P during sorghum growth ($P = 0.37$).

Winter Cover Crops Experiment

During winter cover crop growth, Bray-1 soil P decreased in all cover cropped soils relative to uncropped control soils (Fig. 1B). The resulting Bray-1 soil P was slightly lower in pea (13.3 mg kg⁻¹) and vetch (13.6 mg

Table 4. Correlation coefficients between biomass, N content, and P uptake of winter cover crop green manures and P uptake and biomass of a succeeding sorghum crop. Correlations were conducted (i) using data for all four cover crops and (ii) without data for lupine due to lupine's unique behavior (see text for details).

Perennial forage green manure characteristics	Sorghum characteristics	$P > F^\dagger$	r
Four cover crops			
P uptake	P uptake	<0.0001	-0.85
N content	P uptake	<0.0001	-0.81
Biomass	P uptake	<0.0001	-0.86
P uptake	Biomass	<0.0001	-0.87
N content	Biomass	<0.0001	-0.92
Biomass	Biomass	<0.0001	-0.86
Three cover crops			
P uptake	P uptake	0.12	-0.48
N content	P uptake	0.74	0.11
Biomass	P uptake	0.12	-0.48
P uptake	Biomass	0.47	0.23
N content	Biomass	0.17	-0.43
Biomass	Biomass	0.34	0.30

† Probability of a greater F value.

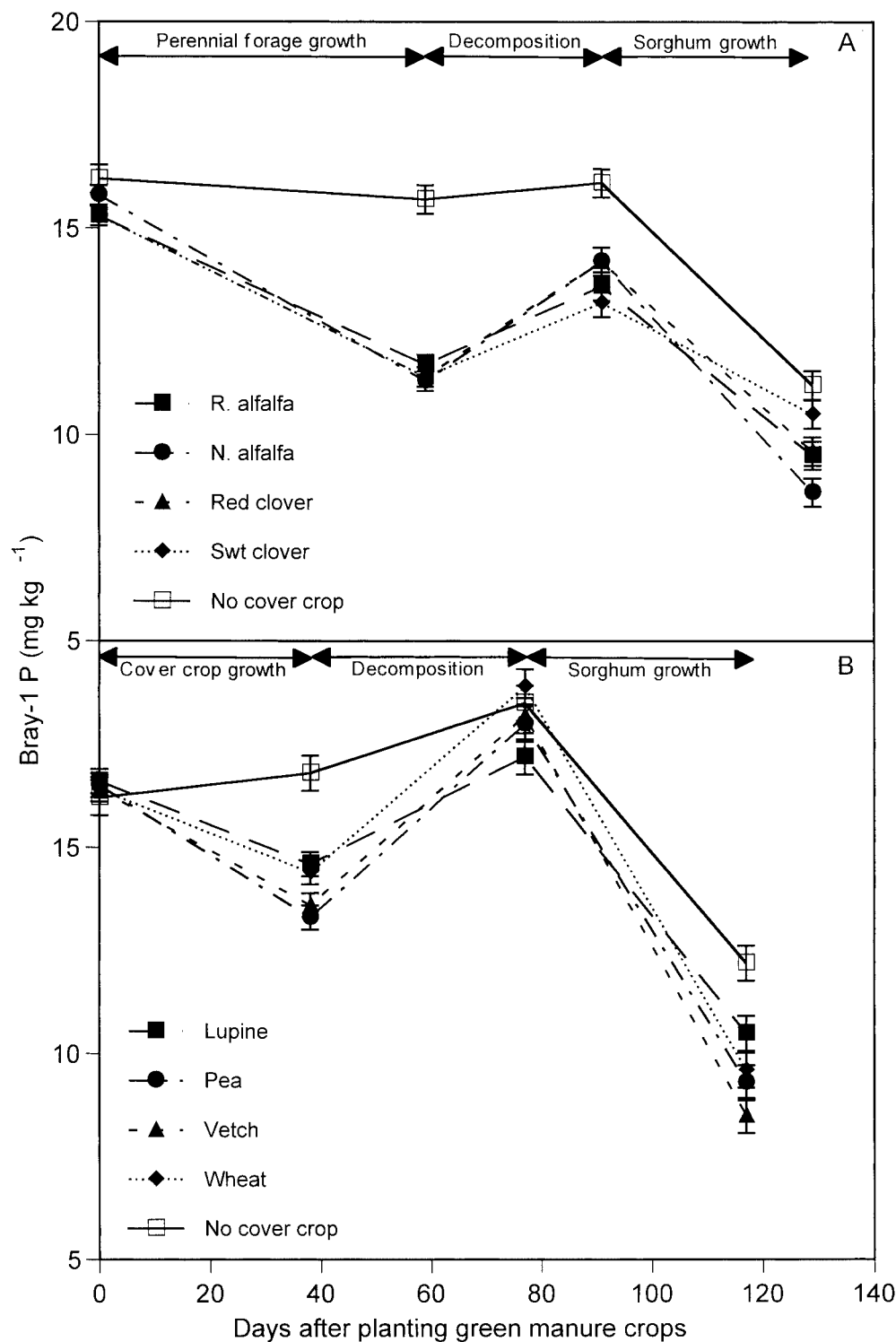


Fig. 1. (A) Changes in Bray-1 soil P during perennial forage green manure crop growth (Day 0 to Day 59) and decomposition (Day 59 to Day 91) and during growth of a succeeding sorghum crop (Day 91 to Day 129) ($n = 8$ replicates for Days 0 and 59; $n = 4$ for Days 91 and 129). (B) Changes in Bray-1 soil P during winter cover crop green manure growth (Day 0 to Day 38) and decomposition (Day 38 to Day 77) and during growth of a succeeding sorghum crop (Day 77 to Day 117) ($n = 8$ replicates for Days 0 and 38; $n = 4$ for Days 77 and 117). Values are adjusted means, and error bars are ± 1 SE, determined using repeated measures analysis.

kg⁻¹) pots than in lupine (14.6 mg kg⁻¹) pots and slightly lower in pea than in wheat (14.4 mg kg⁻¹) pots ($P < 0.0001$). Correlation analyses showed no relationship between winter cover crop adjusted P uptake and the

decrease in Bray-1 soil P during cover crop growth ($P = 0.34$).

During cover crop decomposition, Bray-1 P increased by about 4 mg kg⁻¹ in soils cropped to pea, vetch, and

wheat, which was a greater increase than the 1.6 mg kg⁻¹ increase observed in control soils ($P < 0.05$, LSMEANS = 1.74; Fig. 1B). The slight increase in Bray-1 soil P during lupine residue decomposition (2.6 mg kg⁻¹) was not significantly different from that in the control pots. There was a negative correlation between the change in Bray-1 soil P during winter cover crop decomposition and cover crop adjusted P uptake ($P = 0.06$; $r = -0.48$). This negative relationship was due to lupine's anomalous behavior (high adjusted P uptake, no change in soil P), so we also ran the correlation analysis without the lupine data. In this analysis we found no relationship between cover crop adjusted P uptake and change in Bray-1 soil P ($P = 0.77$). During sorghum growth, Bray-1 soil P decreased in all treatments and these decreases were correlated with sorghum P uptake ($r = -0.74$, $P < 0.005$).

DISCUSSION

For the perennial forages experiment, sorghum P uptake was highest following Nitro alfalfa. This result supports our hypothesis that sorghum P uptake would be highest following green manures with the highest P content. Perennial forage P uptake accounted for 22% of the observed variability in sorghum P uptake ($r^2 = 0.22$). This relationship is particularly noteworthy because the soil used in this experiment was categorized in the medium range for Bray-1 soil P, which indicates that crop yield responses to fertilizer P are expected to be small and inconsistent (Whitney, 1998). Perennial forage N content and biomass did not affect sorghum P uptake.

Our hypothesis also predicts that sorghum biomass would be higher following Nitro alfalfa and sweet clover than following the other perennial forages but we found no differences in sorghum biomass (or N content) following the four perennial forages. Sorghum biomass following perennial forages was higher than in the control treatment but we cannot consider this higher biomass to be a response to the perennial forages since N fertilizer was applied to sorghum at such a late date in the control treatment. Instead, low sorghum biomass in the control treatment is more likely due to the late fertilization date. Tissue N concentrations for perennial forages (equivalent C/N ratios approximately 17, assuming 4.2 g C kg⁻¹) were above levels at which net N mineralization is expected (Sarrantonio, 1994). We assume that sorghum received adequate N following perennial forages.

Perennial forage tissue P concentrations (Table 1) were lower than the commonly reported 2 to 3 g kg⁻¹ net P mineralization threshold level (Yadvinder-Singh et al., 1992) but higher than the 1 g kg⁻¹ threshold level identified by Bumaya and Naylor (1988). Since Bray-1 soil P increased following perennial forage decomposition, our data support Bumaya and Naylor's (1988) finding that net P release can occur when plant residue P concentrations are lower than 2 to 3 g kg⁻¹.

For the winter annual cover crop experiment, our hypothesis predicts that sorghum following lupine would have the highest P uptake and biomass. However, sor-

ghum P uptake following lupine was lower than for any other treatment, including the control, and sorghum biomass following lupine was as low as for the control. Among the other three winter cover crops we found no relationships between cover crop characteristics and sorghum P uptake and biomass. We, therefore, cannot generalize about the four winter cover crops' behavior from these data and we conclude that there is no consistent positive relationship between winter cover crop P uptake and sorghum P uptake and biomass in this experiment. Also, cover crop N content and biomass did not affect sorghum P uptake.

Winter cover crop tissue N concentrations (equivalent C/N ratios 8.8–13.4, assuming 4.2 g C kg⁻¹) were above levels at which net N mineralization is expected (Sarrantonio, 1994) and soil inorganic N levels at the time of sorghum planting suggest that N would not limit sorghum growth following winter cover crops. Differences in N content among winter cover crops did not seem to affect sorghum N uptake, as there were no differences in sorghum N content among the five treatments. However, sorghum biomass was higher following pea, vetch, and wheat than following no cover crop, suggesting that among these three cover crops there was a positive cover crop rotation effect on sorghum biomass.

Although lupine absorbed almost two to three times more P than the other winter cover crops, Bray-1 soil P during lupine's growth changed by the same amount as it did in the other cover crop treatments. This result indicates that lupine is able to take up soil P from non-Bray-1 pools, which is consistent with reports that lupine grows well in low P soils because of its ability to solubilize a significant amount of soil P that is unavailable to other crops (Gardner et al., 1981, 1982, 1983; Gardner and Boundy, 1983; Gerke et al., 1994; Braum and Helmke, 1995).

Low sorghum P uptake and biomass following lupine were probably not caused by N limitation since soil inorganic N was highest following lupine, and sorghum tissue N concentration and N content were as high or higher for sorghum following lupine than for sorghum following the other three cover crops and the N-fertilized control. High soil inorganic N levels indicate that lupine residue decomposition had progressed sufficiently to provide adequate N at the time sorghum was planted. There is some evidence that white lupine can be allelopathic to weeds (Dzyubenko and Petrenko, 1971, cited in Rice, 1984) and that soil organisms stimulated by lupine residue decomposition may have allelopathic effects (Yurchak, 1974; Rice, 1984), but there seems to be no other indication in the literature that lupine might be allelopathic to succeeding crops. In Alabama, where white lupine is sometimes used as a cover crop before planting cotton, cotton yields are always boosted by lupine cover crops as long as cotton is planted about 4 wk after the lupine is killed (E. van Santen, Auburn University, Auburn, AL, personal communication, 2001). We planted sorghum 39 d after lupine was killed in our experiment. Therefore, we do not think allelopathy was involved in decreasing sorghum P uptake in this study.

Numerous other mechanisms may have been respon-

sible for lower sorghum P uptake and biomass following lupine. Perhaps white lupine, the only non-mycorrhizal cover crop in the experiment, suppressed mycorrhizal formation in the succeeding sorghum crop, thereby reducing its P uptake. Inorganic P released during lupine residue decomposition may have been readily read-sorbed (White and Ayoub, 1983; Frossard et al., 1996) to the non-Bray-1 P sites from which lupine had originally mobilized it. Lupine P_o itself could also have been adsorbed to the soil (Tiessen et al., 1994). Some positively charged root exudates increase P adsorption via a complex interaction between the exudates and clay morphology (Kafkafi et al., 1988). Maybe decomposing lupine tissues released compounds with similar P adsorption capacities. Other low molecular weight root exudates can mobilize heavy metals by forming stable complexes (Mench et al., 1988). Perhaps lupine root exudates or decomposition products mobilized heavy metals and the subsequent sorghum crop was subjected to heavy metal toxicity.

In a companion experiment using the same cover crops but soybean as the succeeding crop, we saw no negative effect of lupine on soybean nutrient uptake and biomass (unpublished results). Thus, any effect of white lupine on a succeeding crop may be specific to sorghum, but this possibility requires further study. Further investigation of lupine's role in soil P fertility is warranted given lupine's unique ability to accumulate quickly a large amount of P from recalcitrant, non-Bray-1 soil P pools, and to fix large quantities of N. Experiments have also shown that wheat intercropped with white lupine has greater N and P uptake than does wheat grown alone (Gardner and Boundy, 1983). White lupine is used as an effective cover crop in the southern USA yet we know little about its potentially beneficial effects on P fertility of succeeding crops.

Results from the winter cover crop experiment suggest that plant type seems more important than residue application rate. Others have reported that residue application rate is more important than plant type in affecting soil P availability (Bumaya and Naylor, 1988; Li et al., 1990). These authors added plant residues to soils at rates between 0.1 and 1.0 g kg⁻¹. Assuming that crop residues are incorporated to a depth of 15 cm and that one quarter of cover crop biomass is root biomass (Sustainable Agriculture Network, 1998), a 0.1 g kg⁻¹ residue application rate is equal to aboveground cover crop biomass production of about 16 800 kg ha⁻¹, which is up to five times as much aboveground biomass as can be expected from most cover crops in the Great Plains (Sustainable Agriculture Network, 1998). Thus, results from experiments using these high residue application rates may not be relevant to our experiment or to cover crop residue application rates typically used in the Great Plains. We applied residues at rates more typical for field-grown cover crops in the Great Plains states (0.01–0.05 g kg⁻¹).

Many researchers studying the effect of plant residue applications on soil P bioavailability apply plant residues to soils in which the plants have not been grown (Singh and Jones, 1976; Blair and Boland, 1978; Till and Blair,

1978; Dalal, 1979; White and Ayoub, 1983; McLaughlin and Alston, 1986; Bumaya and Naylor, 1988; McLaughlin et al., 1988a; McLaughlin et al., 1988b; Thibaud et al., 1988; Li et al., 1990). This fact may have an important influence on their results. Although lupine may be an extreme case, roots of other plant species also exude many compounds that can influence P solubility and uptake (Marschner et al., 1986; Jones and Darrah, 1994; Marschner, 1995). We incorporated green manure residues into the same soils in which they were grown. Therefore, each residue was added to a soil that had been treated differently before residue application, as is the case when green manures are used in agricultural settings. Therefore, applying plant residues to soils that have previously been treated equally may not reflect the effects of green manures on soil P bioavailability in field situations.

While changes in Bray-1 soil P were relatively small during the course of the experiments, the general lack of relationship between changes in Bray-1 soil P and P uptake suggests that measuring relative changes in P uptake and release among green manure crops and other organic P sources will require a more sensitive measure of bioavailable soil P (Tiessen et al., 1994). In the perennial forage experiment there was some evidence that perennial forages may have contributed to non-Bray-1 soil P pools since there was a relationship between perennial forage P uptake and sorghum P uptake but there was no relationship between sorghum P uptake and change in Bray-1 soil P during sorghum growth.

We reached different conclusions with respect to our hypotheses in the two experiments, possibly because of our selection of green manure crops in each experiment. The four perennial forages are more closely related to each other than are the four winter cover crops. Therefore, green manure plant characteristics other than P uptake may have been more similar among perennial forages than among winter cover crops. If this is the case, plant characteristics other than P uptake may have been significant confounding factors in the winter cover crop experiment. This difference in plant diversity between the two experiments may explain why we found some support for our hypothesis in the perennial forages experiment but not in the winter cover crops experiment.

The different results in the two experiments may also have been due, at least in part, to running the experiments for different lengths of time, especially the portion of the experiment during green manure growth. Perennial forages were allowed to grow for 59 d while winter cover crops were allowed to grow for only 32 d. Perennial forages were therefore much larger and contained more N and P than the winter cover crops (except lupine) when they were killed. We grew perennial forages for a longer period of time than the cover crops because perennial forages are usually grown for much longer periods of time than are winter annuals in field situations. There are, of course, many differences between greenhouse- and field-grown plants, but if the size of green manure plants at the time they were killed

influenced sorghum P uptake in these experiments, then perhaps field-grown green manures, which are generally grown for longer periods of time than the greenhouse-grown green manures in these experiments, are more likely to influence sorghum P uptake than our greenhouse-grown green manures. Our results provide justification for pursuing similar studies in the field.

Field studies of the effect of green manures on P bioavailability could be conducted within the context of long-term experiments that include plots with and without green manure crops. The capacity of native and agricultural systems to supply P to plants from P mineralization (Cole et al., 1977; Havlin et al., 1984; Oehl et al., 2001) develops over the long-term and may not be detected in the short-term.

CONCLUSIONS

Phosphorus uptake of previous green manure crops in one of two experiments affected sorghum P uptake. Among four perennial forages sorghum P uptake increased with P uptake of the preceding perennial forage crop. Among winter cover crops, however, there was no consistent relationship between P uptake of green manures and P uptake of a subsequent sorghum crop. Lupine, however, which had high N content and P uptake, had no effect on sorghum biomass and a negative effect on sorghum P uptake. Green manure characteristics other than their P uptake can affect P uptake of a subsequent sorghum crop and these complex relationships warrant further study. Green manure P uptake and sorghum biomass were not related in either experiment. Nonetheless, our results indicate that, even in a soil-testing medium in soil P, in which small and inconsistent P fertilizer yield responses are expected, Nitro alfalfa increased soil P bioavailability relative to other perennial forages. Testing the effect of green manures on soil P bioavailability and on P uptake by subsequent crops warrants further research.

Such studies might benefit from using soil P tests that more accurately measure readily mineralizable soil P_o than does the Bray-1 soil P test. Relative increases and decreases in Bray-1 soil P generally were not correlated with relative P uptake among crops. Although changes in Bray-1 soil P among treatments were small, the lack of relationships, in most cases, between Bray-1 soil P and crop uptake suggest that a soil P test that measures P sources made available through microbial activity and other changes in soil characteristics may be more useful for measuring P availability following incorporation of green manures than is the Bray-1 soil P test.

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